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following the instructions of the president, *not to grant any cession of land from the territory of the United States.*

The only comfort which can be derived from this *crying over spilt milk* is that relief which comes with a gush of tears, and from the satisfaction of remembering "what might have been."

N. H. WINCHELL

MINNESOTA HISTORICAL SOCIETY,

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REGENERATION AND THE QUESTION OF "SYMMETRY IN THE BIG CLAWS OF THE LOBSTER"

IN view of several recent articles¹ on the phenomena of symmetrical chelæ in the lobster it seems desirable to offer a few further considerations on the subject of the origin of such structures.

Let us briefly present the nature of the problem. It is a matter of common observation that in the adult lobster the "great" claws are almost invariably asymmetrical with reference to each other; the claw on one side of the body being a "nipper" and the other a "crusher." In a few cases, however, a variation from this normal asymmetry has been discovered, in which the claws instead of differing from each other are very much alike and symmetrical in form. These variations fall into two categories: First, those in which both claws are of the nipper type, and second, those in which the similar claws are both crushers. Two theories for the origin of these relations of symmetry have been presented—first, that they are predetermined in the egg, and second that they may arise through regenerative processes and consequently, are not of necessity wholly determined by congenital factors. Let us consider first the variations from normal asymmetry.

I. *Explanations for Abnormally Symmetrical Claws.*

(a) *Similar Nipper Claws.*—Until very recently in all the authentic cases of similar chelæ, the claws belonged to the first category of the nipper type. Out of over 2,400

¹See especially: (1) Herrick, F. H., 1907, "Symmetry in the Big Claws of the Lobster," *SCIENCE*, Vol. XXV., p. 275. (2) Calman, W. T., 1906, in the "Proceedings of the Zoological Society of London," p. 633.

lobsters² found only three had similar claws. In an examination of some 600 specimens as they came in from the traps at the Experiment Station of the Rhode Island Commission of Inland Fisheries the writer³ found only one lobster with both claws alike. The similar claws of these four cases were all nippers. Theoretically, it may appear quite plausible that a symmetry of this character might be congenital in origin. For in the early development of the lobster both chelæ are alike and similar to the nipper type. At about the sixth stage⁴ normally one of the claws begins to differentiate into a crusher. We might thus have an adult lobster with two nipping claws because they had failed to differentiate in the usual asymmetrical manner. On the other hand, the writer has elsewhere⁵ furnished evidence that this type of symmetry may also be brought about as the result of a process of regeneration.

(b) *Similar Crusher Claws.*—With regard to this second category, however, the congenital theory does not appear to apply so readily. For in this case the development must be conceived as starting in the normal way, and then instead of differentiating asymmetrically both chelæ have passed beyond the normal stages and developed into two crushing claws of the phylogenetically later (according to Stahr⁶ and Przibram⁷) type.

²Herrick, F. H., 1895, "The American Lobster," Bull. U. S. Fish Commission.

³Emmel, V. E., 1907, "Regenerated and Abnormal Appendages in the Lobster," thirty-sixth annual report of the Rhode Island Commission of Inland Fisheries, special paper, No. 31.

⁴Hadley, P. B., 1906, "Changes in Form and Color in Successive Stages of the American Lobster," thirty-fifth annual report of the Rhode Island Commission of Inland Fisheries, Special paper No. 19.

⁵Emmel, V. E., 1906, "Torsion and other Transitional Phenomena in the Regeneration of the Cheliped of the Lobster," *Journ. of Exp. Zoology*, Vol. III., No. 4.

⁶Stahr, H., 1898, "Neue Beiträge zur Morphologie der Hummerschere Jena," *Zeitschr. f. Naturw.*, Bd. 32.

⁷Przibram, H., 1901, "Experimentelle studien über Regeneration, I.," *Archiv. f. Entw.-Mech.*, Bd. XI.

With reference to this latter type of symmetry the following observations serve to emphasize the process of regeneration as a factor in the origin of such abnormal appendages.

Heretofore, a strong presumption has existed that a crusher claw would not be developed on each of the big chelæ, first because, as has already been indicated, the claws of the young lobster are alike and similar to the nipper type, and second, that in the adult lobster, the few cases of symmetrical claws were always of the nipper or embryonic type. Up to 1905 the only case recorded of two crushing claws on a lobster was in a foot-note to Herrick's⁸ description of variations in lobster chelæ: "I have heard of a single case reported by a fisherman where similar crushing claws were developed on both sides of the body" (p. 143). To Przibram writing in 1901⁹ this seemed such an incredible phenomenon that in view of the theoretical reasons indicated above, he concluded that "Der eine Fall von einer Hautung beiderseitigen" crushing claw "von dem Herrick nur vom Horensagen durch Fischer Kenntnis erhielt, wird wohl in der Reich der Fischermythen zu verweisen sein" (p. 333).¹⁰

Since the year 1905 three authentic cases of lobsters with two crushing claws have been placed on record. One of these was reported by Dr. W. T. Calman,¹¹ of the British Museum. He exhibits the photograph of a lobster (*Homarus gammarus*, Linn.) "with symmetrically developed chelæ" which were both crushers (p. 634). Herrick, '07,¹² observes that "this case is, for the present, essentially unique in the literature of the sub-

⁸ *Loc. cit.* (2).

⁹ *Loc. cit.* (7).

¹⁰ I gladly take this opportunity, however, to correct the impression which might be drawn from this quotation. For Przibram in a recent letter has kindly informed me that he has modified his earlier opinion with regard to this matter as the result of his studies on other crustacea. See especially page 215 of his monograph on "Die Heterochelie bei decapoden Crustaceen," *Archiv. f. Entw.-Mech.*, Bd. XIX., 1905.

¹¹ *Loc. cit.* (1).

¹² *Loc. cit.* (1).

ject" (p. 277), but in making this statement he has evidently overlooked my description,¹³ published in 1906, of the two other lobsters with similar crusher claws. The latter two cases of similar crushers were regeneration products, and they are, as far as I am aware, the only cases on record in which the origin of the two crushing chelæ is known, for in neither of the cases recorded by Herrick and Calman has the history of the abnormal chelæ been obtained. A brief restatement of the facts with regard to these regenerated crushers may, therefore, be in place here:¹⁴

One of these cases was obtained in the course of a series of experiments on regeneration made during the summer of 1905, and the other during similar experiments in 1906. In both instances the lobsters had been recently taken from the traps near the experiment station, placed in floating cars and kept in as normal a condition as possible. Let us designate the former as specimen A, and the latter as specimen B.

Specimen A.—The original appendages of this specimen were all normally developed and the animal was in a healthy condition throughout the experiment. The lobster was a female and measured 8 $\frac{3}{8}$ inches in length. On July 26, 1905, both chelæ, and the second and third right walking legs, were autotomously removed. On September 28, sixty-four days after the amputation, the lobster moulted and then measured 8 $\frac{1}{2}$ inches. It had meantime regenerated both chelæ, and the second and third right thoracic legs.

The original left claw of this lobster was a completely developed crusher, characterized by the wide massive claws with an almost entire absence of tactile hairs, and by the presence of broad tubercle-like teeth. The right chela was of a characteristic nipper type with a relatively slender claw, pointed cutting teeth, and a fringe of tactile hairs along the jaws. The right and left chelæ measured 146 and 140 mm. in length, respectively.

Soon after the amputation of these limbs another pair of chelæ began to regenerate from the remaining stump or basipodite. July 18, twenty-three days after the amputation, the regenerating buds both measured 5 mm. in length. By the time

¹³ Emmel, V. E., 1906, "The Regeneration of Two Crusher-Claws following the amputation of the Normal Asymmetrical Chelæ of the Lobster," *Archiv. f. Entw.-Mech.*, Bd. XXII.

¹⁴ For a more detailed description with figures, see *loc. cit.* (3), (13).

the segments of the future limbs were well outlined, attention was drawn to the very similar appearance of the two regenerating structures. Usually, as the lobster approaches the culmination of the moulting period, the regenerating chelæ become so clearly differentiated that a distinction between the crusher and nipper can be readily detected. In the present case, however, no characteristic differences could be observed between the right and left regenerating buds, and, moreover, the general morphological appearance of each suggested that *both* were developing into the crusher type of claws.

After the lobster had moulted, the regenerated chelæ assumed their normal shape and each measured 63 mm. in length. But the regenerative processes had not reproduced the original asymmetrical type of chelæ. The regenerated left claw was a true crusher like the former claw; but the regenerated right claw had the general characters, not of the nipper, but of a typical crusher. A close analysis of the structural features of the regenerated right claw demonstrated that, in all its morphological characters, it corresponded point for point with both the normal and the regenerated crusher of the left side, with respect to the general form, size and proportion, in the shape and arrangement of the teeth, and even in the number and distribution of the tufts of tactile hairs.

Specimen B.—This specimen was an eight-inch male lobster. The original chelæ, as in the preceding case, were also of the normal asymmetrical type, except that in this lobster the right claw was the crusher and the left a nipper. Each chela measured 162 mm. in length.

On August 4, 1906, both chelæ and the second left leg were autotomously removed. Soon after the operation another pair of limbs began to regenerate. By the time the segments of the future appendages were well outlined, the two regenerating chelæ looked very much alike, and the fact that their external characters resembled those of a crusher, suggested that both limbs would develop claws of a crushing type.

By the middle of October, 1906, the lobster had moulted and regenerated both chelæ and the second right leg. Each chela measured 111 mm. in length; they were remarkably similar in structure, and each displayed the character of a typical crushing claw.

In these lobsters, therefore, we have two cases in which the regenerated claws were

symmetrical in form and of the crusher type of chelæ.

With regard to the origin of similar crusher chelæ, Dr. Calman's case has been interpreted as discrediting the regeneration theory for symmetrical chelæ, for in his discussion he says: It has been supposed that this might be due to regeneration after injury, since it is known that in *Brachyura*, on removal of the crushing-claw, a cutting-claw is regenerated. Przibram, however, failed to obtain such "heteromorphic" regeneration in the lobster, and the present specimen throws still further doubt on the regeneration theory, since it possesses a well-developed and quite typical crushing-chelæ on both sides of the body.¹⁵

Herrick in his earlier writing¹⁶ has evidently also favored the congenital theory, for in his discussion of symmetrical claws he states that "there seems to be about as much variation as regards the details here mentioned in normal symmetrical claws as in the abnormally symmetrical ones, and it is probable that in either case the conditions met with are to some extent congenital" (p. 244). In his recent article he discusses both theories without definitely favoring either, and in conclusion states that, "The explanation just offered is based on the assumption that regeneration, following loss, actually occurs in these cases. If there has been no regeneration, we must then fall back upon the view that asymmetry in the great forceps is normally produced by changes which take place in the egg, so the rare condition of symmetry in these appendages may be casually brought about in the same way" (p. 277). With regard to Dr. Calman's case of two crusher claws, Herrick suggests the possibility of getting such a condition through a process of regeneration. But it is important to note that neither of these writers furnishes any experimental proof for the conclusion that symmetrical crushing chelæ have arisen either congenitally or as the result of regeneration. The two cases just described furnish

¹⁵ *Loc. cit.* (1).

¹⁶ *Loc. cit.* (2).

such experimental proof, and establish the fact that the process of regeneration is an important factor in the origin of the symmetrical chelæ occasionally found in the adult lobster.

At present it seems difficult to bring these cases which show the regeneration of two crusher claws under any definite principles of regulation or a developmental mechanics. Evidently they can not be explained as due to a retardation in the process of ontogenetic differentiation, nor does it appear that they can be regarded as a reversion to a phylogenetically older type of chelæ. It is apparently impossible to interpret such a regeneration as a case of "compensatory regulation" in Zeleny's¹⁷ sense, for the regenerated chelæ are almost identically similar in size and form. Nor is it clear that they both can be brought under the category of "reversal" phenomena, if by this term we mean a reversed order of asymmetry. At present, therefore, these cases must rather be described merely as the *substitution* by regeneration of the crusher claw in place of an original nipper chelæ.

II. The Ontogenetic Origin of Normal Asymmetry.

The main question here is, whether normal asymmetry is congenital and wholly predetermined in the egg, or whether it may be influenced by external factors during development.

With regard to this matter Herrick,¹⁸ on the basis of his experiments with the shrimp *Alpheus*, concludes that asymmetry in the lobster "is probably one of direct inheritance, all members of a brood being either right- or left-handed. That is to say, the normal position of the toothed or crushing claw is not haphazard, but is predetermined in the egg" (p. 225). But here again there is a necessity for evidence, for it still remains to be demonstrated that such asymmetry in the lobster is thus predetermined. The results of some experiments made in order to determine whether the crusher could be developed on either side

¹⁷ Zeleny, C., 1905, "Compensatory Regulation," *Jour. of Exp. Zoology*, Vol. II., No. 1.

¹⁸ 1907, *loc. cit.* (1).

of the body by making appropriate mutilations during the larval stages, *i. e.*, at a period when the chelæ have not yet differentiated into nipper and crusher—may be here introduced. Although these experiments are still in progress, some of the data is already significant because it tends to support a different theory than that of direct inheritance.

On July 24, 1906, two groups of second-stage larval lobsters were mutilated. In group A, the right chela was amputated, and in group B, the left chela was removed in each specimen. The lobsters were kept in separate compartments and precaution taken to keep a careful record of mutilations, moults, and regenerations for each individual. Such an experiment is especially difficult because the naturally great mortality of larval lobsters when kept in artificial conditions is greatly increased by the injury attending mutilation, but I succeeded in rearing beyond the fourth stage four specimens in group A, and nine specimens in group B. After each moult the regenerated chela was

GROUP A: RIGHT CHELA REMOVED

Specimen	Stage	Date of First Mutilation	Number of Moults	Character of the Chelæ		
				Date	Right	Left
1	2d	July 24	Six	Sept. 29	Nipper	Crusher
2	2d	" 24	Six	Oct. 6	Nipper	Crusher
3	2d	" 24	Six	Sept. 29	Nipper	Crusher
4	2d	" 24	Six	Nov. 8	Nipper	Crusher*

GROUP B: LEFT CHELA REMOVED

1	2d	July 24	Six	Oct. 27	Crusher	Nipper
2	2d	" 24	Six	Sept. 29	Crusher	Nipper
3	2d	" 24	Six	Oct. 13	(?)†	Nipper
4	2d	" 24	Six	Oct. 19	Crusher	Nipper
5	2d	" 24	Six	Oct. 19	Crusher	Nipper
6	2d	" 24	Six	Oct. 19	Crusher	Nipper
7	2d	" 24	Six	Oct. 19	Crusher	Nipper
8	2d	" 24	Six	Oct. 19	(?)†	Nipper
9	2d	" 24	Six	Sept. 22	Crusher	Nipper

* This specimen was very late in displaying any asymmetrical differentiation, but by November 18 the left chela became somewhat broader, showed a characteristic crusher curve in the dactyl and tubercle-like teeth in the proximal region of each jaw.

† Up to date showed no evidence of having differentiated into a crusher.

invariably amputated. The limb on the opposite side of the body was thus given every possible advantage with regard to growth, in order to see whether this chela could be made to differentiate into a crusher. The data so far obtained for these specimens is in the table given above.

From this table it will be observed that in over 90 per cent. of the specimens the chelæ have already differentiated asymmetrically, but in no case for group A did a crusher develop on the right side, or in group B, a crusher on the left side. The evidence for specimens Nos. 3 and 9 is at present neutral, for they still appear to retain their embryonic symmetry, and it remains to be seen at the next moult, which will occur during the spring, whether they too will finally develop a crusher on the right side or not. At any rate, this experiment clearly shows that *in all cases where the chelæ have differentiated far enough to display asymmetrical characters, the crusher has developed on the chela which was given the greater opportunity for growth; i. e., on the side which was not mutilated.*

The results so far attained, therefore, establish a strong presumption that the "right- or left-handedness" of the lobster may not be entirely predetermined in the egg. If these results are confirmed by further experiments, it ought to furnish convincing proof that the asymmetrical relation of chelæ in the lobster may under certain conditions, at least, be determined by other than hereditary factors.

This result is especially interesting in view of the fact that in the adult lobster we do not seem to meet with the phenomenon of reversal or compensatory regulation which Zeleny¹⁹ and Przibram²⁰ have found in other crustacea. In the course of my experiments I have mutilated over 200 adult lobsters in which the normal asymmetrical limbs were autotomously removed and preserved for each specimen, but in no case did a crusher ever regenerate on the side which had originally carried a nipper and at the same time *vice*

versa for the nipper. It has been suggested that possibly one reason why we do not get a typical reversal in the lobster is because the asymmetry of chelæ consists in a greater qualitative differentiation than in the case of the crabs and some other decapod crustacea, consequently, a true reversal in the lobster would involve more fundamental morphological transformations than in the case of these other forms. On the other hand, in the larval lobster the chelæ are very similar both qualitatively and quantitatively, and the results of our experiments seem to indicate that the symmetrical relations of the organisms are at this stage in a much more plastic condition.

We may summarize, then, this discussion of regeneration and the origin of symmetry as follows: First, positive evidence has been advanced that the process of regeneration is an important factor in the origin of symmetrical chelæ. Second, the results of the foregoing experiments on the larval stages establish a strong presumption that the right- or left-handed asymmetry of the lobster, instead of being entirely hereditary, may be influenced during ontogenetic development by external factors.

V. E. EMMEL

ANATOMICAL LABORATORY,
BROWN UNIVERSITY,
PROVIDENCE, R. I.,
March 6, 1907

DIE BACK OF THE PEACH TREES (*Valsa leucostoma* Pers.)

DIE back is a serious enemy of the cherry orchards of Germany. It is especially destructive in the districts along the Rhine. It is also reported as being parasitic on the stone fruits of Australia. Professor F. C. Stewart, of the New York Agricultural Experiment Station, was the first American to call attention to the parasitic nature of this fungus. Ellis and Everhart in their 'North American Pyrenomycetes' state that this organism is found on peach, plum and almond trees in Carolina, Pennsylvania, New Jersey and probably throughout the country where the trees are found.

Experiments at this station show that it

¹⁹ *Loc. cit.* (17).

²⁰ *Loc. cit.* (7).